

**The Natural History and Behavior of *Hymenoepimecis argyraphaga*
(Hymenoptera: Ichneumonidae) a Parasitoid of *Plesiometa argyra*
(Araneae: Tetragnathidae)**

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Abstract.—Larvae of the koinobiont ectoparasitoid *Hymenoepimecis argyraphaga* Gauld used a series of different adaptations as they matured to hold onto the abdomen of their host spider, *Plesiometa argyra*, its web, and the larval cocoon: the first instar did not leave the egg chorion, which was glued to the spider by the female wasp when she oviposited; the second instar used two pairs of ventral abdominal protuberances to help hold onto both the first larva's molted cuticle and to what was probably a sheet of coagulated spider hemolymph that adhered to the larva and to wounds that it made on the spider's abdomen; the early final instar grasped the shed second instar cuticle that remained attached to the coagulated hemolymph with the ventral surface of its abdomen; and the late final instar used a row of mobile dorsal protuberances with sharply curved spines that grasped lines of a unique web that the larva induced the spider to spin just before killing it, and then the larva's own cocoon silk. The pupa used a pair of toothed protuberances at the tip of the abdomen to stay at the upper end of its cocoon. Other aspects of the wasp's biology that are described include infanticide by adult females; aculeate-like lack of use of the ovipositor to oviposit; manipulation of host web-spinning behavior, apparently by means of a fast-acting larval secretion with long-term effects; manipulation of host bleeding; alternative tactics in attacks on spiders; use of pheromones by females to attract males; cocoon spinning behavior; and a bias to parasitize female rather than male spiders.

Although Ichneumonidae is undoubtedly one of the largest of all animal families, remarkably little is known about the behavior of the larvae. Excluding studies of foraging behavior, adult behavior is also poorly studied (e.g., Hanson and Gauld 1995). The neotropical polysphinctine pimplines are no exception. The more derived polysphinctines are known to be koinobiont ectoparasitoids of spiders (Gauld 1995, Wahl and Gauld 1998), and several European species were observed in careful detail by G. C. Bignell (1898) and E. Nielsen (1923, 1928, 1929, 1935). There is apparently only a single study of a neotropical species, that of Fincke et al. (1990) on *Hymenoepimecis robertsae* Gauld (for probable identification see Gauld et al. 1998). The general natural history of this

species resembles that of some European polysphinctines. It is an external koinobiont on a spider, the tetragnathid *Nephila clavipes* (L.). The female temporarily paralyzes the host by stinging it in the cephalothorax, and then glues an egg on its abdomen. Spiders with a wasp egg or a young larva are active, and build apparently normal prey capture webs and feed while the larva feeds by sucking the spider's hemolymph and gradually matures. The spider's webs become more irregular and reduced one to two days before the larva kills it and constructs its pupal cocoon, which is attached to the spider's web. A second species, *H. tedfordi* Gauld, parasitizes another tetragnathid spider, *Leucauge marinae* Keyserling (Gauld et al. 1998), but nothing more is known about

Table 1. Degree of development of eggs in the ovaries (6–7 ovarioles/ovary) of female wasps of different ages (N = number of wasps; W = white eggs apparently ready to be laid, Y = yellow, still-immature eggs; uric acid determined on arbitrary scale of 0–3).

Age of wasp outside cocoon (hrs)	Mean length and color of eggs (mm)				Amount of uric acid	N
	Largest (basal) egg in each ovariole	Color	Second largest egg	Color		
6–12	0.15 ± .18	Y	0		2, 3	2
24	0.22 ± .20	Y	0		1, 2, 2	3
approx. 36	0.82 ± .04	W	0.27 ± .02	Y	0	1
approx. 60	0.59 ± .27	W/Y	0.08 ± .17	Y	1, 1	2
approx. 72	0.84 ± .02	W	0.68 ± .21	Y	0, 1	2
approx. 84	0.84 ± .05	W	0.56 ± .14	Y	0, 0	2

its behavior. The present observations concern a third, newly discovered species, *H. argyraphaga* Gauld (Gauld 2000).

MATERIALS AND METHODS

Field observations were made in January and February of 1999 and 2000 in the undergrowth of plantations of approximately 10–15 m tall African oil palms (*Elaeis guianensis*) near Parrita, Puntarenas Province, Costa Rica (elevation about 20 m). Spiders were checked for parasites in the field with a 10× hand lens while holding the spider by its legs, and some wasp attacks were observed using a 2× headband magnifier. Spiders and immature stages of the wasps were transported to San Antonio de Escazu (1300 m), and reared there. All observations were at room temperature, and durations of some immature stages of the wasps may be slight overestimates, due to the lower temperatures in San Antonio. Dissections and measurements were made using recently killed individuals in saline solution. Bleeding and coagulation were studied by poking a minuten pin through the abdominal cuticle of mature female spiders.

Video recordings of behavior were made using a Sony CCD-TR700 camcorder with +7 closeup lenses. Voucher specimens of wasps have been deposited in the The Natural History Museum, London, the Museo de Insectos of the Universidad de Costa Rica, and the U. S. National Museum of Natural History. Spe-

cies names follow Fitton et al. 1988, and Gauld et al. 1998. The species observed by Bignell (1898) is cited as an undetermined polysphinctine because of confusion regarding its identity (M. Shaw, pers. comm.).

RESULTS

Adults

Maturation of eggs.—Dissections of females kept with access to water and honey after they emerged as adults showed that females emerged without any well-developed eggs, but with massive fat bodies that contained large amounts of small white pellets (presumably uric acid) (Table 1). Over the next 3–4 days the fat and uric acid diminished, and the yellow developing eggs gradually grew and changed to large, whitish eggs that were apparently ready to lay. Eggs matured one by one, rather than synchronously, both within a given ovariole and in different ovarioles.

Sexual behavior.—Males were seen repeatedly in the field. They flew slowly, and did not stay in any given area. They repeatedly hovered near the tips of leaves at the tops of undergrowth plants. Their flight patterns were inappropriate to encounter pupal cocoons, which were generally lower and deeper in the vegetation. Males showed no signs of sustained aggression when they encountered each other, although one male flew into and

knocked another from his perch on a leaf tip.

Two interactions between males and females were observed in the field. Both involved virgin females that had recently emerged from their cocoons. Each female rested on the side of her cocoon for at least 90 min, where she eliminated small white masses (presumably uric acid) and periodically cleaned herself. No males approached the females as they rested on their cocoons. Eventually each female flew 1–2 m and landed on the tip of a leaf about 1.5 m above the ground, near the top of the undergrowth. Close inspection of one of the females using the headband magnifier as she rested on the plant failed to reveal any obvious sign of pheromone emission (extension of abdomen, drops of liquid, eversion of membranous sac). Nevertheless, one female had only been on the leaf for about 65 s when a male arrived. The wind was too slow and erratic to determine whether or not he arrived from downwind. He landed directly on the female, and immediately curled his abdomen forward ventrally and copulated. After 5–10 s, the female began to walk, the male gave a couple of brief buzzes of his wings, the pair separated, and both wasps flew away.

The second virgin female moved from one leaf tip to another twice before being approached by a male. This male flew persistently from tip to tip of the pinnules of a palm leaf that was just downwind of the female, landing briefly on each. Then he flew about 1 m upwind and returned to search again. On his third or fourth approach the male encountered the plant on which the female was resting, and landed near her. She immediately took flight, and the male continued to investigate leaf tips in the vicinity for about 1 min more before moving on.

Hunting for spiders.—I witnessed 14 attacks (eight successful) in their entirety, and parts of five others. The early stages of all attacks were similar. The wasp hov-

ered about 10–30 cm from the spider, facing toward it as it rested at the hub of its more or less horizontal orb for several seconds. Usually the attack was launched from about 10–15 cm above the spider. The wasp darted rapidly at the spider and grasped it through the web with her legs. The wasp did not consistently strike from downwind of the spider, and in one case she first hovered at one side of the spider, then flew over it, turned 180° to face it again, and attacked from the other side. Thus at least the final stage of host localization appeared to depend on visual rather than chemical cues. Wasps were more likely to attack larger spiders (see section below on parasitism rates).

There was always a brief struggle during which it was not possible to resolve exactly what was happening; probably the wasp jabbed rapidly and forcefully with her ovipositor while she grasped the spider with her legs. When I was finally able to resolve the animals' positions (usually after 10 s or less), the wasp's ovipositor was inserted into the anterior end of the spider's cephalothorax; in four cases it was apparently thrust into the spider's mouth, in two it was just to the side of one chelicera, and in another it was on the anterior side of the spider's first coxa. This first long sting lasted for up to 120 s, during which the spider's struggles gradually became less vigorous. In two attacks on relatively small spiders the sting was only about 10–20 s. After withdrawing her ovipositor, the wasp performed a series of apparent jabs with her ovipositor, and in two cases she inserted it again into the spider's cephalothorax. By this time the spider rested completely immobile at the hub of its web (Fig. 1). Paralysis generally lasted for approximately 5–10 min.

The wasp then positioned herself under the spider's abdomen, facing posteriorly (Fig. 1), and bent her abdomen ventrally and repeatedly wiped, jabbed and rubbed with the distal portion of her ovipositor for as long as several minutes over the an-

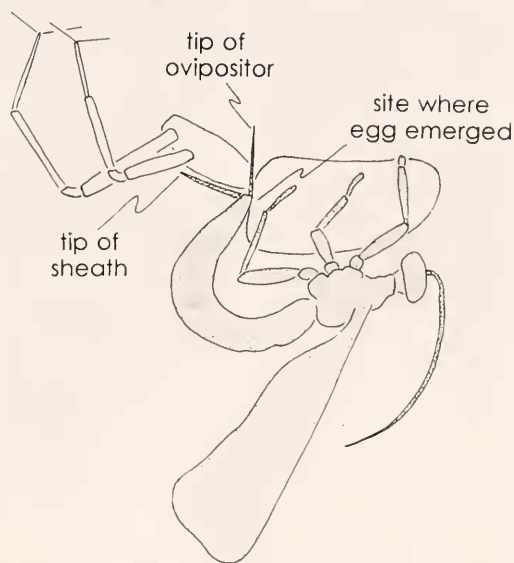


Fig. 1. Diagrammatic illustration of a female wasp hanging on paralyzed spider at the hub of its web and ovipositing at the point indicated (drawn from field notes; it is not certain whether the wasp's tarsi held the spider, as in the drawing, or the web just above it).

terior and dorsal surface of the spider's abdomen. These probing movements probably served to locate, perhaps to sting, and to dislodge the eggs or larvae of previous wasps that had attacked this spider. In one case, repeated probing movements of the ovipositor in the vicinity of a first instar or early second instar larva may have included one or more insertions of the ovipositor into the larva, and they finally resulted in the larva being levered off of the spider's abdomen and onto the middle portion of the wasp's ovipositor. The wasp then knocked off the larva to the ground with cleaning movements, and soon afterward laid an egg of her own. In two other cases an egg (identity confirmed by subsequent collection) was moved onto the middle of the ovipositor and then fell to the ground.

Of 16 parasitized spiders collected in 1999 with eggs or first instar larvae on their abdomens, four gave further evidence that larvae are sometimes removed:

there were one or more groups of larval feeding scars on portions of the abdomen that were inaccessible to the current larva in two cases, and there were larval feeding scars but no larvae and only an egg in two others. In contrast, only one spider was doubly parasitized, carrying both an egg and a second instar larva. Similar data from 2000 gave even more dramatic evidence of infanticide. Of 55 mature female spiders, nearly half (26) had at least one patch of feeding and bleeding scars on her abdomen (the total of additional patches was 43; the maximum on one spider was four). Only three spiders were doubly parasitized. It should be noted that these data undoubtedly underestimate the frequency of infanticide, because removal of eggs from hosts cannot be detected using feeding scars.

Finally the wasp oviposited. Holding her ovipositor sheaths elevated dorsally and her ovipositor pressed against the anterior surface of the spider's abdomen (Fig. 1), she pressed the tip of her abdomen near the surface of the spider's abdomen briefly. The egg emerged from the tip of her abdomen (and *not* from the tip of her ovipositor), and adhered to the spider's abdomen. Within about 30 sec after ovipositing the wasp flew away. In no case did a wasp give any sign of attempting to feed on the spider. Although eggs were generally placed on the anterior dorsal surface of the spider's abdomen, the exact sites varied widely (Fig. 3). The oval egg was glued tightly on its ventral side to the spider's abdominal cuticle. Two eggs which were observed being laid and then inspected periodically hatched between 48 and 72 hours later.

An incomplete observation of one interaction indicated that the wasps have an alternative hunting strategy that depends on deceiving the spider. When they were first encountered, the spider was resting at the edge of its orb, and the wasp was hanging immobile from radii in the free zone near the hub, facing downward with

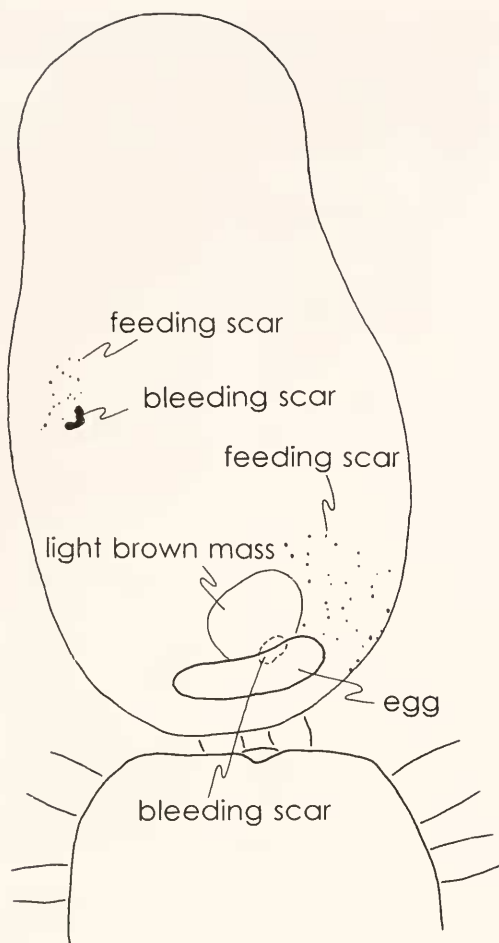


Fig. 2. Evidence of two infanticides. The anterior surface of the abdomen of a *P. argyra* spider bears a wasp egg, and two arrays of feeding and bleeding scars (dark spots) that were presumably produced by wasp larvae that had hatched from eggs laid previously, but that were then removed when subsequent female wasps attacked this spider.

most or all of her legs extended stiffly. The wasp appeared to be either dead or paralyzed, and a gentle nudge of the wasp with my finger confirmed that she was completely immobile. She remained motionless until the spider returned to the hub about 5 min later. As the spider arrived at the hub, however, there was a sudden tangle of legs and it quickly became clear that the wasp's ovipositor was inserted near the spider's mouth. Soon the

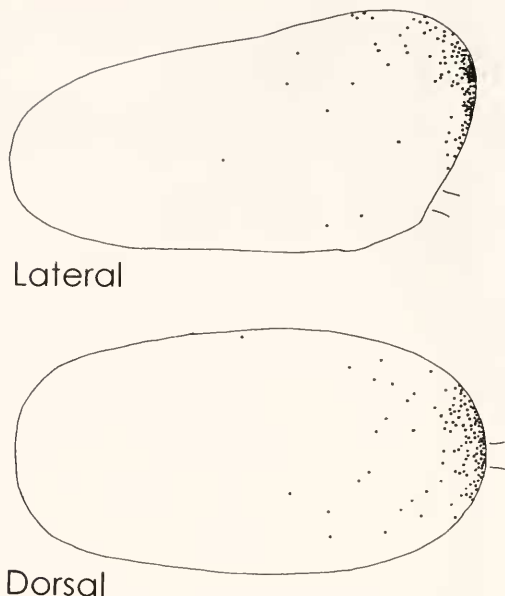


Fig. 3. Schematic representation of 125 sites of the anterior ends of egg and the bleeding scars of the larva on the spider's abdomen in lateral and dorsal views.

spider became immobile, and the wasp, which had fooled both the spider and me by playing dead, proceeded to oviposit.

Wasps also showed a certain flexibility in oviposition behavior. When one spider began to move after the wasp had spent several minutes attempting to remove an egg, the wasp moved to its anterior end and apparently stung it again, then resumed egg removal.

Failed wasp attacks illustrate possible kinds of selection on spiders to avoid attacks. In one case the spider's orb was inclined so that much of its surface was between the wasp and the spider as the wasp hovered above and to the side of the spider; when the wasp finally struck, it hit and was arrested by the orb before reaching the spider, the spider moved away, and the wasp flew on. In two other cases (one first seen after the interaction had already begun), the spider hung from its dragline about 10–15 cm below the hub, and when the wasp struck from above it hit and was arrested by the orb, and thus

did not reach the spider. The wasp then hovered nearby, and the spider twice climbed very rapidly to the hub but immediately dropped again. Finally the spider dashed to the edge of the web, and the wasp flew on. The presence of web threads between the spider and the wasp that were not right next to the spider thus appeared to reduce the likelihood that a wasp's attack would succeed. A final failure occurred when a gentle wind apparently made it more difficult for the wasp to hover steadily near the spider, and she eventually crashed into the web and then flew away. Windier sites may thus be safer for spiders.

Larvae

First instar.—The first instar larva apparently burst open one end of the egg, but only its anterior end emerged from the chorion. Its posterior end remained lodged inside the chorion, and thus attached to the spider. The first instar larvae possessed neither the ventral nor the dorsal structures used by later instars to hold onto the spider and its web. A small brown spot or feeding scar (see below) appeared on the spider's abdomen just beyond the edge of the chorion of recently emerged larvae. The subsequent gradual accumulation of feeding scars on the spider's abdomen, which were always restricted to the vicinity of the larva's head, indicated that the larva fed at small holes it made in the spider's abdomen (Figs. 2, 4). As the larva grew, it gradually protruded more and more from the egg chorion. The head, the entire thorax, and the first two to three abdominal segments were free by the time the larva was ready to molt to the second instar, and by then there were 8–10 feeding scars on the spider's abdomen. The first instar lasted between 58 and 69 hours ($N = 2$).

First instar larvae were able to remain attached when the spider molted, as evidenced by two pale, soft newly-molted adult spiders each having a first instar lar-

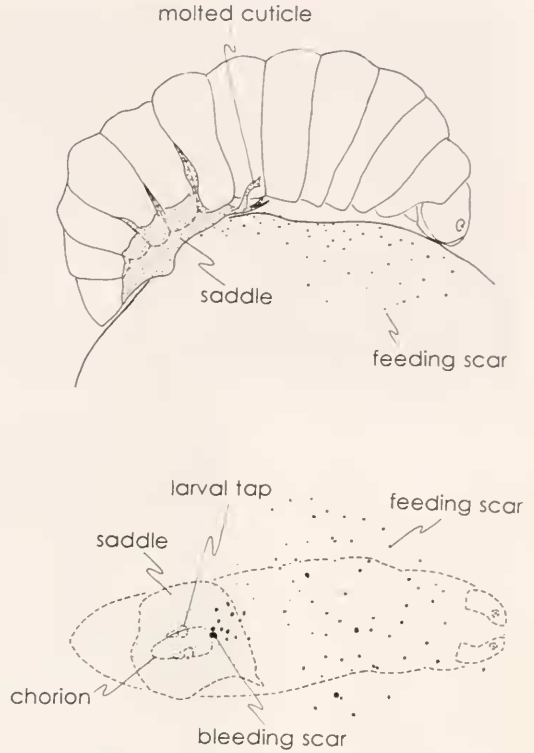


Fig. 4. Pattern of brown scars on the abdomen of a spider carrying a second instar larva in lateral view (above) and ventral view, looking outward through the spider's cuticle (below). The sites of insertion of the larva's taps were not visible, and were determined by subsequent dissection.

va attached to its abdomen. In both cases (and in two other spiders) a portion of the cuticle of the previous instar (usually the dorsal portion of the cephalothorax plus a wrinkled portion of the abdomen) was attached to the spider's abdomen, apparently at a bleeding scar (Fig. 4).

Second instar.—The transformation from first to second instar was not witnessed, and the probable series of events was reconstructed from preserved specimens. The newly molted second instar larva was completely outside the collapsed egg chorion. The larva's ventral surface rested on the flattened, shed first instar larval cuticle, and this cuticle in turn rested on a large, stiff sheet of brown amorphous material (Figs. 4, 5) (the "saddle" of Nielsen

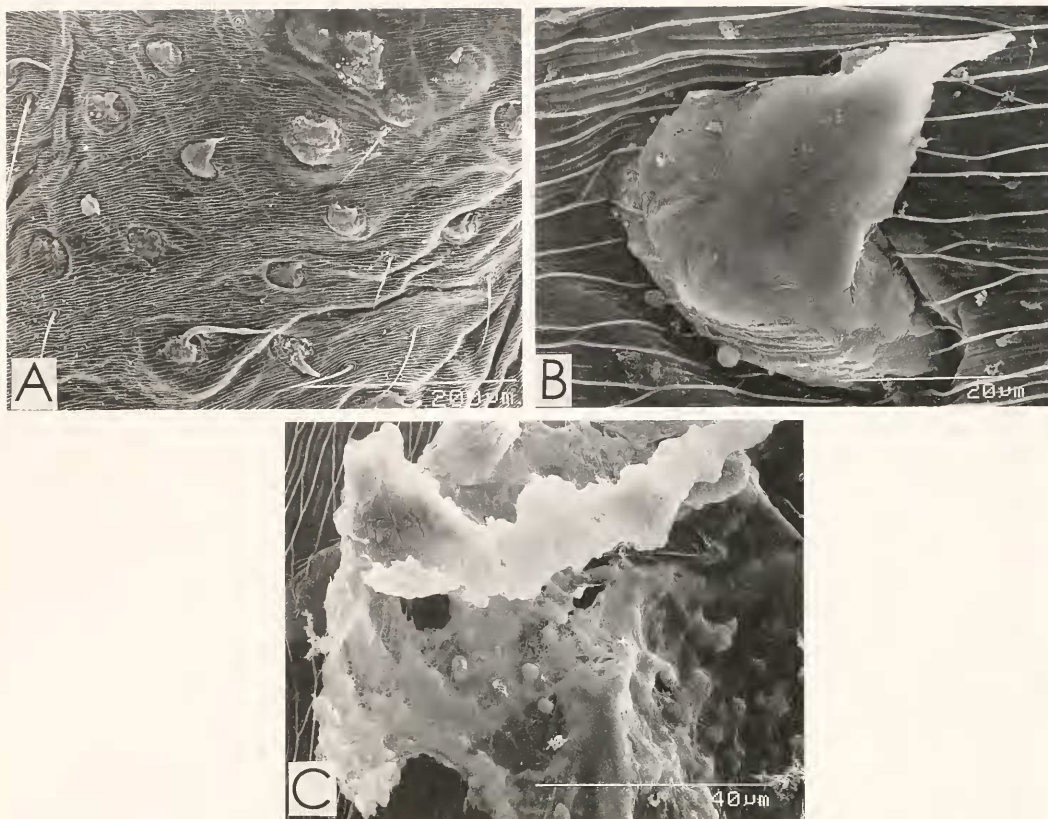


Fig. 5. Micrographs of apparent feeding scars (A and B) and saddle material (C) of a second instar larva on the corrugated abdominal cuticle of a spider. Many feeding scars were produced into more or less conical protuberances of different shapes (A). A closeup view (B) shows that the scar material (presumably coagulated hemolymph) flowed over the corrugated abdominal cuticle around the perforation before hardening. The "saddle" material is amorphous, and is not a shed larval skin.

1923). The empty egg chorion was on the inner surface of the saddle that contacted the surface of the spider's abdomen. The saddle was probably composed of coagulated hemolymph, and had a different form in each parasitized spider. It was tightly attached to the spider's abdomen near the open end of the egg. The anterior end of the shed larval cuticle was near the anterior edge of this sheet, indicating that molting probably involved a split of the first instar's cuticle along the dorsal midline of most of the larva's body, rather than a rearward sloughing of cuticle as occurred at pupation (see below).

The saddle adhered to both the ventral surface of the larva on its outer side, and

to the spider's abdominal cuticle on its inner side, and could be peeled away intact from both except at the central attachment area. Here it was attached tightly to the spider's abdomen at several brown spots that were similar to the feeding scars mentioned above but larger (Fig. 4). In some cases projections of the saddle extended into the larva's intersegmental grooves (Fig. 4), indicating that the saddle had been a liquid at some time after the larva molted. Two pairs of protuberances ("taps" of Nielsen 1923) on the ventral surface of the larva's segments 8 and 9 were inserted deeply into the saddle (and perhaps also the shed skin) (Fig. 4). They adhered so tightly to the saddle that it was

difficult to separate the larva from it without damaging the taps.

The second instar larva apparently continued feeding as before, as brown feeding scars gradually accumulated on the side of the spider's abdomen on which the larva's head rested. Many feeding scars were produced externally into more or less conical shapes whose tips pointed anteriorly on the abdomen (toward the larva's head) (Fig. 5). The spider's pattern of coloration, which was due to soft tissues under the transparent abdominal cuticle, was often (though not always) intact in areas with feeding scars. Thus larvae probably usually consumed hemolymph, rather than digesting other internal tissues.

When the spider's abdominal tissue was dissected away, there were no inward extensions of either the feeding scars or the attachment spots; all were relatively smooth on their inner surfaces. Smaller feeding scars were concentrated nearer the egg (where the larva presumably fed when it was smaller—Fig. 4). The feeding scars had a remarkably regular distribution, with larger spaces between larger scars (Figs 2, 4).

Saddle-like puddles of hemolymph did not form at experimental wounds (approximately 0.1 mm diameter) made by puncturing the abdominal cuticle with a fine pin, despite the fact that these holes were larger than feeding scars (about 40 μm in dia—see Fig. 5). In nearly all cases the hole was immediately sealed by a small plug when the pin was withdrawn. This plug, which was little more than the diameter of the hole, was initially liquid when touched with the pin, but hardened to a solid within 10–15 s, and darkened to a light brown color. In two cases in which a small sheet (up to about 0.3 mm in diameter) of hemolymph emerged from the wound before a plug formed, the sheet did not turn dark brown, but instead acquired a nearly transparent golden color. The inner surfaces of these wounds, revealed by dissecting away underlying tis-

sue after the specimen was preserved in alcohol, were smooth and dark, similar to those of feeding scars.

The number of second instar larvae prior to their final day (below) in collections made in 2000 was approximately equal to the number of eggs and of first instar larvae (62 second instars, 73 eggs, 57 first instars). Assuming that the egg stage lasts about 2.5 days and that the relative numbers of the different immature stages were fairly constant over the space of a few weeks (supported by the similarity in numbers in the surveys made on 28–30 Jan. and 9–10 Feb, 2000— $\text{Chi}^2 = 2.7$, $\text{df} = 3$, $p > 0.4$), this suggests that the second instar normally lasts two to three days in nature. It can also last much longer, however. The second instar lasted 46 days in one case in which the spider was kept captive with only infrequent feeding. Spiders carrying first and second instar larvae occurred on apparently normal orbs in the field (Eberhard in prep.).

The true number of larval instars is not certain. Fitton et al. (1988) speculated that all pimelines may have five larval instars, on the grounds that *Pimpla* does, with "the middle three being very similar and hard to distinguish". If so, then the stages designated here as first and second may actually represent three or four stages that I was unable to distinguish. The distribution of the widths of the head capsules of 81 larvae (Fig. 6) did not clarify this. There were two peaks within the range of sizes classified here as first instars, while several final instar larvae (which can be recognized unequivocally by the dorsal tubercles covered with curved spines) were substantially smaller than several others which were clearly in the previous instar (the curved spines were visible, but were covered with a transparent layer of cuticle). It may be that head capsule width is not constant within an instar, as some sclerites may be connected by elastic membranes.

Final ("third") instar.—There were sev-

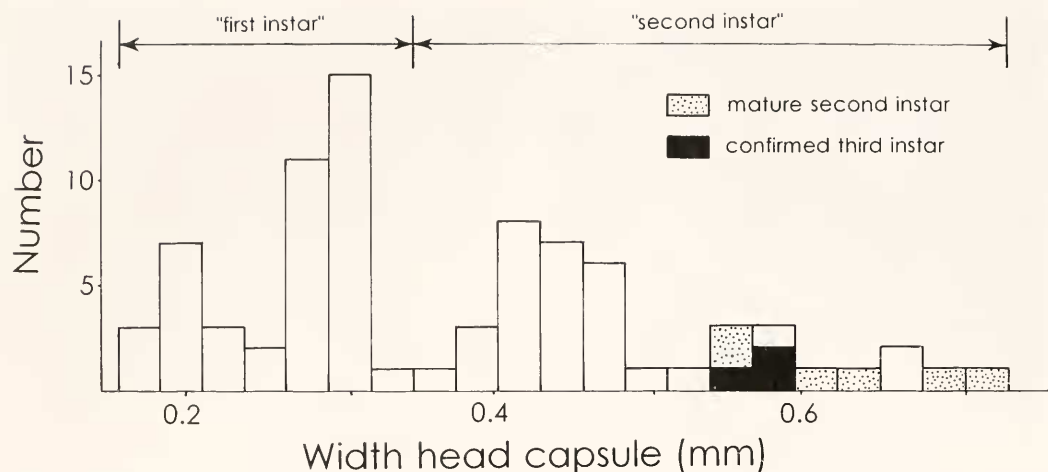


Fig. 6. Distribution of head capsule widths of 81 larvae, and approximate limits of classifications of larval instars used in this study. "Confirmed" final (supposed third) instar larvae had hooked spines on dorsal tubercles; "mature" second instar larvae had hooks that were clearly visible under the larva's dorsal cuticle.

eral differences between second and third (final) instar larvae. The dorsal surfaces of eight segments (3–10 posterior to the head) of the final instar, which had been smooth in previous instars, each had a retractable two-lobed tubercle whose tips were covered with curved spines (Fig. 7). There was a pair of taps on the ventral surface of segments 8 and 9 as in the second instar, but they were free (Fig. 8), and not embedded in the saddle. The shed cuticle of the second instar formed a compact sheet bent into a cup. It adhered tightly to the saddle, apparently where the

taps of the cuticle of the second instar were inserted. The saddle, in turn, still adhered tightly to the spider's abdomen. The larva grasped the posterior edge of the sheet of second instar cuticle between its final (13th) segment and the bulging ventral margin of its penultimate (12th) segment (Fig. 8C). In addition, the larva's head capsule was substantially different (Fig. 9).

The final instar was relatively brief. All larvae raised to final instars or collected in the field as swollen second instars or as final instars killed the spider the following

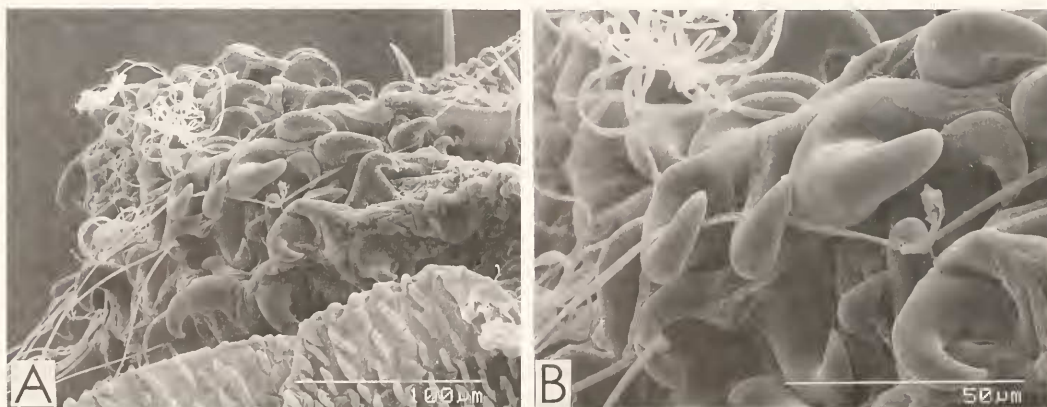


Fig. 7. Hooks on a dorsal tubercle of a final instar larva that have snagged tangled spider silk.

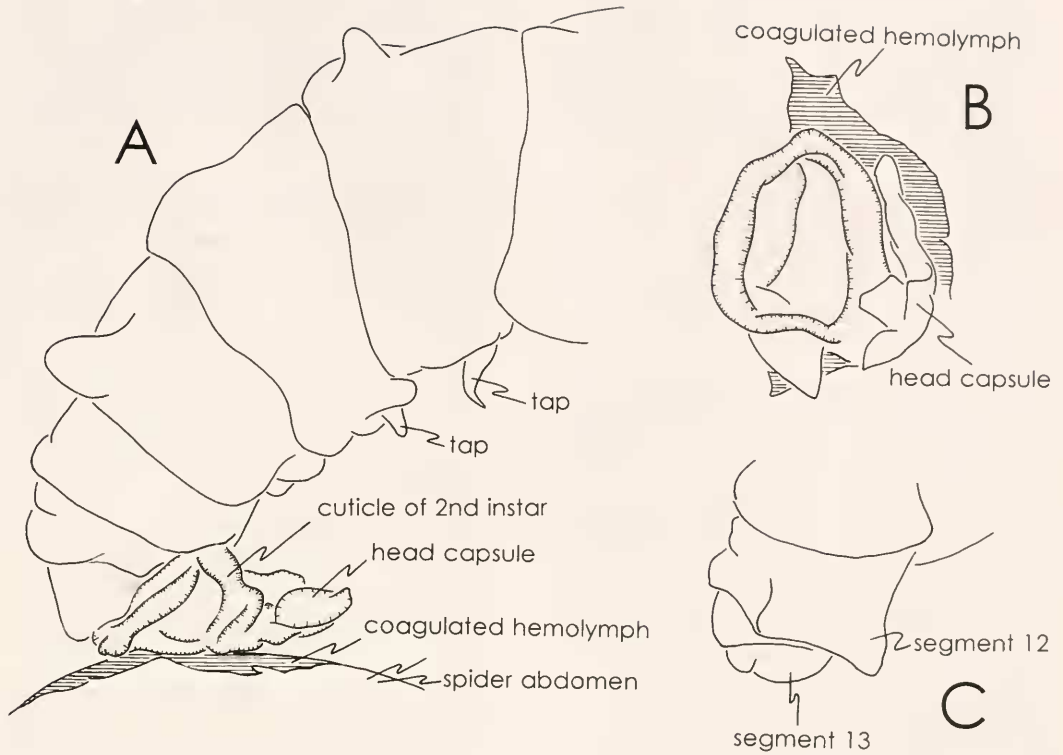


Fig. 8. (A) Attachment of the final instar larva to the spider's abdomen, seen in lateral view. (B) Dorsal view of the cup-shaped mass of larval cuticle. (C) Lateral view of the posterior tip of a larva removed from its attachment to the spider, showing the protruding ventral surface of segment 12 that gripped the edge of the cup of larval cuticle.

night. An estimate from field collections of swollen last day second instar larvae and early final instars on spiders in 2000 was in accord with the estimate of a duration

of only one day or slightly less (only 18 individuals, as compared with 73 eggs and 57 first instars).

The final day in the spider's life was eventful. At least some spiders built an orb of apparently normal design and size in the morning, but during the day the second instar larva grew to an estimated one quarter to one third of the volume of the spider's abdomen. At about 23:00–01:00 the spider built a modified "cocoon web" of a few highly reinforced radial lines that was especially appropriate to support the cocoon the larva would build the next evening. In two cases the larva repeatedly extended its body nearly straight while the spider built the cocoon web.

The cocoon web and the behavior employed to build it are described elsewhere



Fig. 9. Antero-lateral view of head capsule of final instar larva.

(Eberhard in press, in prep.). Briefly, the spider used one portion of one subroutine of frame line construction over and over to build a small number (mean 3.8 ± 1.4 , $N = 39$) of radial lines, each of which is a cable composed of many individual lines. This web did not resemble any prey capture, resting, molting, or egg sacs webs normally built by *P. argyra*. Experimental removal of larvae showed there to be a complex, long-term effect on the spider's behavior that is probably mediated chemically. Typical cocoon web construction followed in three cases when a swollen second instar larva was removed from a spider that had been kept in a confined space until about midnight, when it would probably have begun cocoon web construction. These spiders were still alive the next day, and the next evening they each built a second typical cocoon web.

Thirteen other spiders from which the larvae were removed between 22:00 and 02:00 built structures that were neither normal orbs nor cocoon webs. Three of these spiders were observed building. They placed radial lines from the hub to the edge using the behavior used to construct typical cocoon webs (Eberhard in prep.), but also broke and reeled up these lines while moving back toward the hub. The final products were sparse networks of more or less radial lines in which there were large accumulations of reeled up silk (fluff) near the hub. All of these spiders were also alive and active the next morning.

Soon after it finished the cocoon web, the parasitized spider became immobile. All of nine spiders were dead or completely immobile by 03:00 (in one checked under the microscope, the heart had stopped beating), and the larva had lifted the anterior portion of its body above that of the spider to grasp the lines of the web with its dorsal protuberances (see below). The posterior portion of its body remained attached to the saddle. The larva proceeded to suck the spider dry over the course of

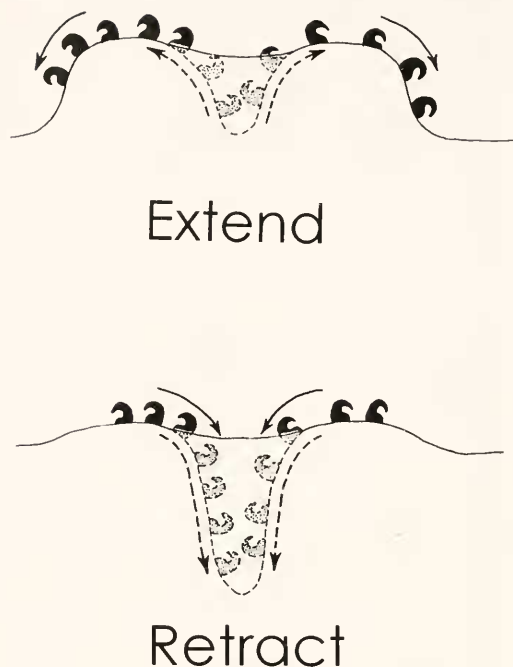


Fig. 10. Diagrammatic representation of the movements of the curved spines at the tip of a turret that caused lines to be snagged when the tubercle was everted (above), and release of lines when it was retracted (below).

the morning, feeding first on the spider's abdomen and then on its cephalothorax.

The mechanism by which the larva grasped and released lines with its hook-covered dorsal tubercles was revealed by observations under a dissecting microscope. The tubercles were extremely mobile, and could be extended so that the distance of their tips from the dorsal surface of the larva's body was up to about one third of the diameter of the body. They could also be retracted rapidly so that the entire tubercle and all of its hooks disappeared completely into a pocket on the dorsal surface of the larva's body. Because the spines near the tip of each tubercle were sharply curved, eversion of the tubercle resulted in a grasping effect, as lines were snagged by the curved spines (Figs. 7, 10). The spines released their holds on lines when the tubercle was retracted into the larva's body.

Coordination of tubercle movements was complex. When the larva moved its anterior end, the anterior-most three tubercles often contacted the web only sporadically. When the tubercles were out of contact they were often everted and retracted simultaneously. In contrast, the more posterior tubercles, which usually held onto threads and supported the larva's weight, moved less often and sequentially. When the larva moved its entire body forward or backward, each tubercle that was holding silk released its hold by retracting, everted toward the next tubercle where it seized silk, and the next tubercle then released its hold and was everted toward the next, and so on. These stepping movements swept along the larva's body rapidly, and it sometimes stepped with several tubercles in a second.

Feeding by a final instar larva on a dead spider was observed under a dissecting microscope. The first stage of a feeding bout involved apparent searching and hooking of the mouthparts against the surface of the abdominal cuticle. I was not able to discern any pattern to these movements, nor any responses to the brown feeding scars already present. Finally, sometimes after minutes of such searching, the larva's head came to rest at a particular site where it apparently began to produce a hole.

After a minute or so, the larva began to suck. The rhythmic movements of its head were reminiscent of those of a nursing human infant (Fig. 11). Approximately once every second the larva pulled its head slightly away from the abdomen without breaking contact with its mouthparts, then sprang slightly toward it again. In one case it was possible to see the flow of the spider's tissues through the transparent cuticle of the abdomen as the larva sucked. Clumps of abdominal tissue flowed steadily into the larva's mouth. Two timed feeding bouts lasted about 30 min. They ended when the larva pulled its head away and rested immobile for sev-

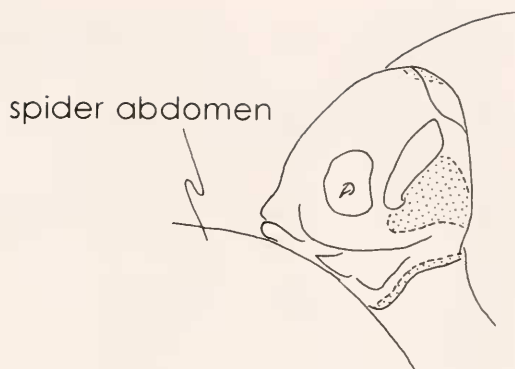


Fig. 11. Diagrammatic representation of the head of a feeding larva; the stippled areas pulsed as the larva sucked.

eral minutes. When the larva withdrew its head after feeding, there was a small amount of clear liquid on the surface of the spider which quickly dried up; no hole was visible, nor did a brown spot form.

On three occasions it was clear that the larva interrupted sucking and that a clear liquid flowed from its mouth into the spider for several seconds. This liquid formed a small pool around the point where the larva's head contacted the abdomen, and it also flowed under the cuticle, as deduced from brief movements of spider tissue away from the larva's mouthparts. Presumably the clear liquid contained digestive enzymes.

When feeding ended, the larva freed itself from the now more or less empty but intact cuticle of the spider, and it dropped to the ground below. This process was not observed directly, and it was not clear whether the larva actively unhooked the spider's tarsal claws from the web. The saddle was still attached to the discarded carcass of the spider, and bore the imprint of the larva's last two abdominal segments (Fig. 8). In two cases the discarded carcass of the spider represented about 50% of the larva's weight: larvae which weighed 15.7 and 26.2 mg discarded carcasses that weighed, respectively, 6.1 and 10.4 mg.

The now somewhat greenish larva hung motionless, curled ventrally as it held the

web with its dorsal tubercles, for the rest of the daylight hours. Larvae in the field were remarkably coordinated in killing and consuming their hosts. All but one of 13 final instar larvae found before 13:00 were still feeding on the dead host, while all of 11 found between 13:00 and 17:00 had dropped the spider and were resting immobile at the hub of the cocoon web.

Cocoon construction began soon after darkness fell (about 18:40). The process of first attaching the cocoon's suspension line to the spider's web, then extending the line below the web, and then forming the walls of the cocoon was accomplished as the larva slowly inched backward over a period of up to an hour or more. The larva maintained a hold on silk lines with its dorsal tubercles at all times. At first it held onto the silk of the spider's cocoon web, then later onto the suspension line of its cocoon.

The larva produced a silk line (or lines?) from its head by pulling away from a point where the line was attached, and then attached this line to others by tapping or rubbing its head against them. The first lines were attached repeatedly to the lines at the hub of the spider's web, and were often somewhat dispersed. Gradually they condensed into a single multi-stranded line as the larva moved backward a few millimeters. The suspension line of the cocoon was produced by a simple sequence of movements repeated over and over (Fig. 12A). First the larva attached its line to the spider's web, and drew out a line by moving its head downward. Usually it paused immobile for several seconds, and then moved its head farther, toward the posterior end of its body, which was bent anteriorly. The head usually dabbed or scraped repeatedly against the posterior portion of the body, gradually touching points more and more toward its dorsal surface. During the last few scrapes it often dragged its mouthparts across its rearmost dorsal tubercle. Probably these movements often resulted

in snagging the line on the tubercle. The larva then extended the rear portion of its body downward, thus probably pulling more silk, and it moved its head back up to contact the spider web above and make another attachment there. The usual duration of one complete cycle was about 5–10 s.

By repeating this sequence of spinning movements over and over, the larva gradually produced a bundle of lines that ran from the attachments to the spider web down to the rear end of its own body and back up to the web again. This bundle would form the suspension line of the cocoon. The suspension line was lengthened when the larva grasped the bundle with the dorsal tubercles, moving rearward along the bundle, and then resuming spinning movements. Eventually the upper attachments of spinning movements were to the suspension line itself rather than to the spider's web.

The final stage of cocoon construction also involved a simple pattern repeated over and over (Fig. 12B). The larva moved its head to touch the edge of the bundle of lines already spun near its lower end, then pulled away a short distance and then moved back to touch the edge again slightly farther up, and repeated this behavior until it reached the suspension line, then bent downward again to begin the next series of attachments near the bottom edge of the bundle. The larva thus gradually extended the bundle laterally to form a bag-like sheet that enclosed the posterior portion of its body. Later the bag was gradually extended upward to enclose the upper portion of its body also. The bag was closed by addition of lines to its inner surface, about 4–5 hrs after cocoon construction began. Once the bag was closed it was more difficult to observe the larva's behavior, but it was clear that it sometimes turned 180° to face downward and add more lines to the bottom of the cocoon. Cocoon construction contin-

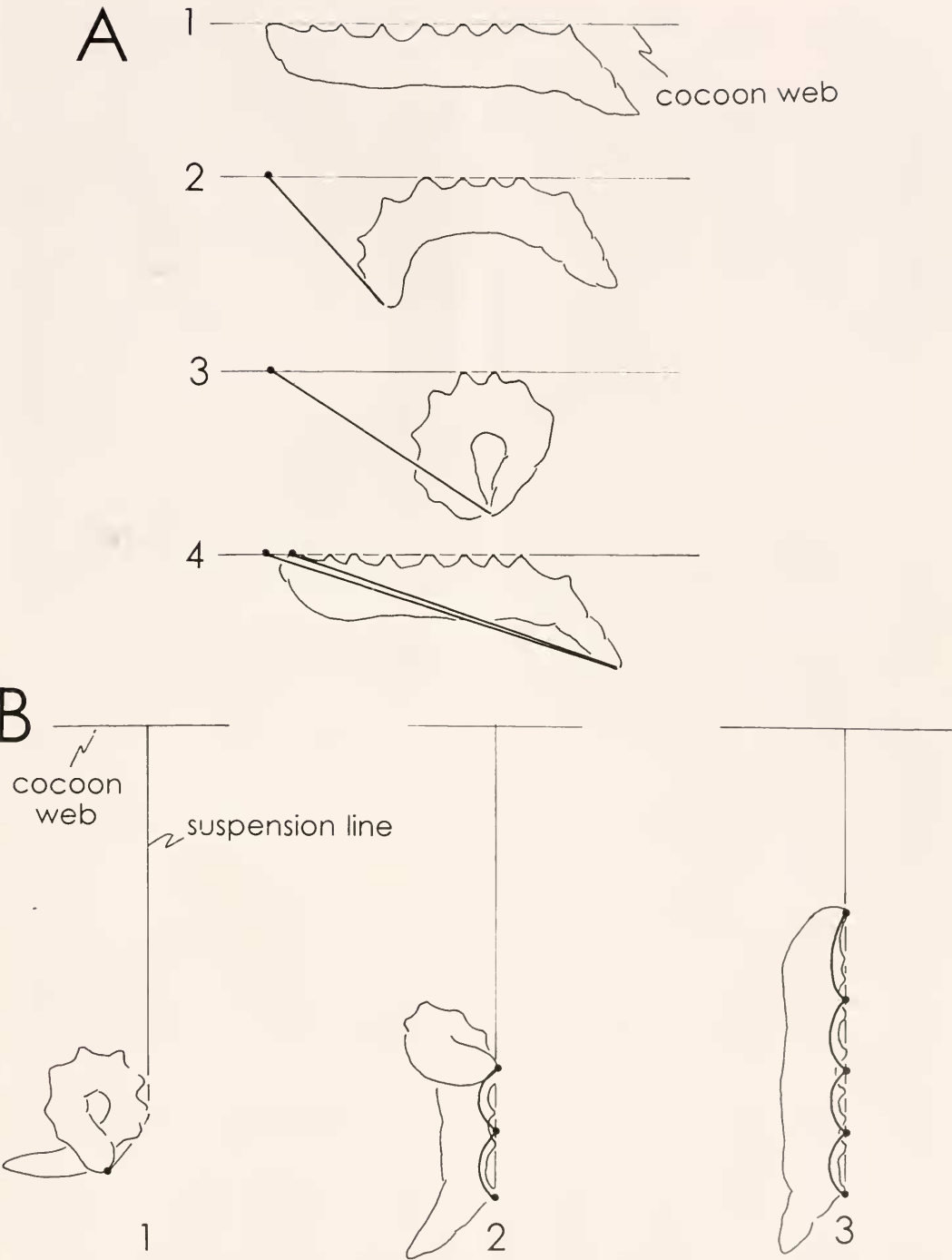


Fig. 12. The sequence of movements as a larva built the suspension line of the cocoon (A) and when it began the cocoon itself (B).

ued through the night and the following morning.

Cocoons spun in captivity were all very light yellow in color, and gradually darkened over the next day or so. Those kept in closed containers out of the light were especially pale. Some of those found in nature were dark yellow, while most were bright orange. About 36–65 hrs. after cocoon construction began, the larva ejected its meconium, which generally fell through the circular hole at the bottom of the cocoon (Gauld et al. 1998). One larva molted to a pupa between 4 and 5 days after killing its host.

Pupa

Pupal behavior could not be observed directly, except for the short series of rapid dorso-ventral contractions of the abdomen usually made when the pupa was disturbed. Indirect evidence suggests that the pair of toothed prominences near the tip of the pupal abdomen, which were immobile, served to engage the tip of the abdomen against the inner wall of the cocoon, and thus hold the pupa at the upper end of its cocoon. All of seven living pupae checked by cutting a slit in the side of the cocoon were wedged at the upper end of the cocoon (the pupa occupied only an estimated average $83 \pm 6\%$ of the length of the cocoon). All pupae observed in cocoons were oriented with the head upward, and the circular emergence slit made by the adult was always at the upper end of the cocoon. Presumably this position served to keep the pupa's posterior end away from the meconium or the shed larval skin that was sometimes present at the bottom tip of the cocoon. Four adults emerged 10–12 days after cocoon construction, so the pupal stage lasted about a week. A total of 26 males and 38 females were raised from field-collected cocoons (not significantly different from 50:50 with Chi² Test).

Other aspects of natural history

Rates of parasitism.—Mature female spiders were approximately ten times more heavily parasitized than were mature males (42.9% of 203 females compared with 6.9% of 72 males in 1999; 66.4% of 125 females vs. 3.2% of 62 males in 2000). The rate of parasitism of mature females earlier in 1999 (27–30 Jan) was lower than that later (2–5 Feb.) the same year (26.5% of 83 females compared with 50% of 120 females— $p < 0.001$ with Chi²). In contrast, the first survey in 2000 showed a higher rate for mature females than for the second survey that year (84.2% of 57 females on 28–30 Jan., vs. 51.5% of 68 on 9–10 Feb., $p < 0.001$ with Chi²). The rates of parasitism of mature males did not differ significantly for the two surveys in either year (7.1% of 28 compared with 6.9% of 44 in 1999, 3.1% of 32 vs. 3.3% of 30 in 2000).

Mature females were also more heavily parasitized than were immatures. In the first survey of 2000, 84.2% of mature females, but only 50.8% of 63 penultimate females, 39.5% of 43 penultimate males, and 25.7% of ante-penultimate nymphs were paralyzed (all rates were lower than that for mature females, $p < 0.001$ with Chi²; ante-penultimates were less parasitized than penultimates, $p = 0.033$ with Chi²). Similarly, penultimate spiders showed less evidence of infanticide (25 cases in 73 spiders, compared with 43 cases among 55 mature females, $p < 0.001$ with Chi²).

Enemies of the wasp.—Mortality in the cocoon was relatively low. Seven *Conura* of two different species, one in the *immaculata* group of the subgenus *Ceratosmicra*, and the other in the *vau* group of the subgenus *Conura* (Chalcididae) were raised from 105 inhabited cocoons collected in the field in 1999, and 4 of 85 empty cocoons had *Conura* sp. pupal skins, giving a total rate of 5.8%. An eighth female *Conura* was captured after being first seen resting on the side of a cocoon in the field.

Two days later this cocoon contained a young pupa of *H. argyraphaga*, suggesting that the late larval or early pupal stage of the host was parasitized. Two chalcids that pupated in captivity each had a dead *H. argyraphaga* pupa in the same cocoon, and three empty cocoons collected in the field that had a pupal cuticle of *Conura* also had the remains of a *H. argyraphaga* pupa.

Other field mortality of stages in cocoons, presumably due to predators, was noted as removal of the entire cocoon from the cocoon web (8 cases), or complete removal of the cocoon's contents (associated with a large hole in the side in two cases, and with multiple small ragged holes in two others). Two mature female spiders in the field carried dead first instar larvae, but the cause of death was not clear.

Two adult *H. argyraphaga*, one male and one female, were found dead at the hubs of orb webs of the araneid *Gasteracantha cancriformis* (L.), despite the fact that the wasps seem to be chemically defended. Even recently emerged adults less than four hours old released a pungent odor when grasped between the fingers (neither large second instar larvae nor their host spiders had any perceptible smell or taste). One tug of war between a larva and a salticid spider at the hub of a new cocoon web resulted in the larva's loss of the dead spider, and nearly resulted in predation on the larva.

One further predatory event may have been an artifact, but it illustrates another potential danger to the wasp. A penultimate instar male spider with a swollen second instar larva was placed in a plastic bag in a more or less cramped position. An hour or so later, the spider was feeding on the anterior end of the larva, which was still attached posteriorly to the saddle. In no other case did a parasitized spider exhibit any behavior directed toward the larva on its abdomen.

DISCUSSION

Chemical manipulation of the host.—Larvae of *H. argyraphaga* manipulate both the behavior and the physiology of their hosts. The changes in the spider's behavior which resulted in the production of the otherwise unique, strong "cocoon" web that is particularly well designed to sustain the wasp's cocoon, involved induction of the first steps of one subprogram of orb web construction that were repeated over and over to the exclusion of others (Eberhard in press, in prep.). Experimental removal of larvae showed that these behavioral changes occurred as a result of a fast-acting substance or substances with long-term effects introduced into the spider just before the larva molted to the final instar. It appears that the larva's induction of one type of building behavior and repression of others may represent separate effects, as their manifestation was partially uncoupled by early removal of the larva (Eberhard in prep.). Induction by the final instar during cocoon web construction seems unlikely, due to both the softness of the final instar's pale head capsule soon after molting, and the complete cocoon webs obtained after the mature second instar was removed. In contrast, the death of the spider soon after the cocoon web was finished probably resulted from material injected by the final instar larva just after the cocoon web was finished, when it began to feed; spiders did not die when the larva was removed just prior to this molt.

Manipulation of spider bleeding occurred when the larva molted from the first to second instar, and resulted in the production of the saddle. The form and the position of the saddle suggest that liquid hemolymph emerged in unusually large amounts from the large holes in the spider's abdomen and did not immediately coagulate as usual (one saddle was about 0.9×1.5 mm, while the largest puddle of hemolymph produced by wound-

ing with a minuten pin was only about 0.27 mm in diameter). These holes were probably made just before the first instar larva emerged from the egg chorion to molt, because the newly molted second instar larva would have had a soft head capsule, presumably incapable of biting through the spider's cuticle. Judging by the apparent difficulty that the larger final instar larva had in perforating the spider's relatively tough cuticle, it probably took the first instar larva many minutes to make these large holes. The spider's hemolymph must have coagulated only slowly, and was evidently still liquid after ecdysis occurred, since saddle material sometimes flowed part way up the side of the second instar larva's cuticle (Fig. 4). Liquid hemolymph may have helped the larva adhere to the spider during the delicate period after it had abandoned its egg but was still a first instar and thus lacked grasping structures. The extensive flow of hemolymph and the long delay before it coagulated contrast with the small plugs of rapidly coagulated hemolymph at puncture wounds made with a fine pin. Presumably the larva added something to the spider's blood which retarded coagulation.

One other possible manipulation was the inhibition of molting by host spiders. The evidence is only indirect, however. Despite the fact that wasp larvae were able to remain attached when their host molted (as also occurs in other polysphinctines—Nielsen 1923), and that the rate of parasitism of penultimate male spiders was not significantly different from that of penultimate females (39.5% of 45 penultimate males versus 50.8% of 63 penultimate females in 2000), the rate of parasitism of mature males was only about a tenth of that of mature females the same year. Of 32 parasitized penultimate and ante-penultimate spiders reared for two weeks, not a single spider molted. The only evidence that spiders molted after being parasitized involved wasp larvae that

were very small when they were found, apparently soon after the spider's molt. Perhaps these larvae had not been hatched long enough to inhibit the molt.

Comparisons with related wasps.—There are many points of similarity between the behavior and natural history of *H. argyraphaga* and *H. robertsae* (Fincke et al. 1990), and with polysphinctines of other genera (Bignell 1898, Nielsen 1923, Fitton et al. 1988, Gauld et al. 1998). Females of *H. robertsae* may also attack spiders at the hubs of their webs, sting the spider in the cephalothorax to produce a temporary paralysis (Fincke and colleagues witnessed only what were apparently aftermaths of attacks, however), and lay an egg on the anterior surface of the abdomen. The female wasp also moves the ovipositor back and forth over the spider's abdomen (for up to five min) prior to ovipositing, and thus may also remove previously deposited eggs or larvae. Fincke et al. (1990) found four doubly parasitized spiders, however. Thus *H. argyraphaga* is the only species yet found in which it is certain that females kill the offspring from previous attacks on the host. The selective advantage of infanticide seems obvious. Only one of probably several hundred cocoon webs seen in the field had two cocoons, and only one of these two produced a wasp. A second doubly parasitized spider was killed and consumed in captivity by the larger larva, while the smaller larva fell to the ground (still alive) with the discarded cadaver of the spider.

Similar use of the egg chorion to hold onto the spider occurs in *Acrodactyla madida* (Haliday) (= *Polysphincta clypeata*), though Nielsen's (1923) drawings indicate that the egg of this species is also used by larger larvae, rather than only the first instar as in *H. argyraphaga*. The dorsal tubercles ("warts") of the final instar are similar in form and placement to those of *Zatypota albicoxa* (Walker) (= *Polysphincta eximia*) and *Polysphincta tuberosa* Gravenhorst (Nielsen 1923). The two pairs of ven-

tral taps on segments 8 and 9 of the final instar larva of *H. argyraphaga* also resembled those of most of the species studied by Nielsen (1923), except that he recorded three pairs (on segments 7, 8 and 9) in *P. tuberosa*.

The use of the sharply hooked setae on the tubercles to seize silk lines was apparently identical in all other species observed. Although Fincke et al. (1990) made no direct observations of larval behavior of *H. robertsae*, their Fig. 3 clearly shows dorsal tubercles on a large larva, leading to the supposition that they also have curved spines and are used to hold onto the spider's web. Bignell (1898) seems to have been correct in stating that lines were released by retracting these tubercles rather than by extending them, as also occurs in a pimpline ichneumonid that is probably fairly closely related to Polysphinctini, *Tromatobia oculatoria* (Fabricius) (Nielsen 1923) (Nielsen 1923 may have been mistaken in describing the opposite process of releasing by extending in *Z. albicoxa*).

Only some details of how larvae of *H. argyraphaga* hold onto the host spider resemble descriptions of other species. Insertion of the paired ventral taps into a mass of material (the saddle) that adheres to the spider's abdomen, as described for second instar *H. argyraphaga*, has been seen in several other species (Nielsen 1923, 1935), though no difference was noted between second and final instar larvae. Nielsen (1923) stated that the cuticle of the first instar larva of *Z. albicoxa* was "glued to the host", but this was not true for *H. argyraphaga*. In conjunction with this idea, Nielsen supposed that the saddle consisted of larval exuviae (Nielsen 1923, 1935), and this has been reiterated by later authors (e.g., Fitton et al. 1987, 1988). It seems likely, however, that the portion of the second instar's saddle that adhered to the host was coagulated spider hemolymph as in *H. argyraphaga* (Figs. 4, 5), rather than first instar larval cuticle. In fact Nielsen (1923) mentioned that wounds

might be involved in allowing the larva to adhere to the spider.

None of the descriptions of other species mentioned the final instar larva's change to hold onto the shed cuticle of the second instar with its terminal segments instead of its taps, as seen in *H. argyraphaga*. The mature larva's ability to release the spider in all of the species in order to pupate (presumably by relaxing the muscles that squeezed the shed cuticle), and the especially active movements of the posterior tip of the larva during the only molting process that has ever been observed directly (Nielsen 1923: 148–149 on *Z. albicoxa*; "... the repeated attempts at fixing made by the hind end ..."), suggest that similar changes may occur in other species.

Both Nielsen and Bignell also noted that the larva of respectively *Zatypota* and an undetermined polysphinctine utilized the posterior part of the abdomen to pull out silk lines during cocoon construction, although their descriptions differ in details. It is not clear whether these differences were due to differences between species or, as supposed by Nielsen (1923), to differences in the precision of observations. The cocoons of *H. robertsae* were similar in form and color to those of *H. argyraphaga*. Increases in the duration of the larval stage when the host is feeding poorly, as in *H. argyraphaga*, probably also occurs in other species (Nielsen 1923).

Females of *H. robertsae* were also larger than males, as is common among pimplines (Gauld et al. 1998), implying that ovipositing females fertilize or refrain from fertilizing the egg on the basis of the size of the prey. If molting by the host is inhibited by *H. argyraphaga*, then the size of the spider when it is attacked will correlate with the size of the resulting wasp. Both species avoided parasitizing mature males of their hosts, probably for different reason. Mature male *N. clavipes* are probably too small to produce an adult *H. robertsae* (Fincke et al. 1990). Mature males of

P. argyra were, in contrast, not too small to produce adult wasps. For instance one moderately small mature male spider weighed 14.0 mg, somewhat more than the 13.7 mg of a parasitized penultimate male and 12.1 mg of a parasitized antepenultimate male. Mature male *P. argyra* were only parasitized about a tenth as often as mature females, however (totals of 5.1% of 136 males and 51.8% of 328 females in the two years). It was clear that both of the mature males parasitized in 2000 had been attacked when they were in the penultimate instar, because part of the cuticle from the previous instar adhered to the male's abdomen at the feeding scar below the larva in both cases.

The reason for lower parasitism of mature males was presumably either because female *H. argyraphaga* rejected mature male spiders, or were less able to find and attack them. Active rejection seems likely, because mature males of *P. argyra* often chase off smaller individuals and use their orbs to capture prey (10 of 11 males checked for this detail were at the hubs of an orb). Thus mature males are probably often exposed to hunting female wasps. Active avoidance of males may be advantageous to the wasps because at least sometimes mature males fail to construct a cocoon web (Eberhard in prep.), thereby probably making the wasp's cocoon more vulnerable to enemies.

The mating system of *H. argyraphaga* apparently differs from that of at least some other ichneumonids in which males are attracted to sites where females are emerging. Males of *H. argyraphaga* were apparently not attracted to emerging or recently emerged females as they rested on their cocoons, but quickly approached females after they flew to nearby vegetation. Females probably actively release a long-range attractant pheromone. Males appeared to concentrate their searching behavior at the tips of leaves of prominent plants, suggesting that they also use visual stimuli. The very short copulation of *H.*

argyraphaga was similar to that observed (in captivity) in *Schizopyga podagrica* (Nielsen 1935).

One possible difference between *H. argyraphaga* and *H. robertsae* is that the latter apparently does not induce the spider to spin a highly modified cocoon web. Perhaps induction of behavioral changes has been lost, as the larger size of *Nephila clavipes* and the corresponding greater durability of the mesh lines near its orbs (which often remain more or less intact for several days without repair by the spider—W. Eberhard unpub.) may make a modified web to support the cocoon unnecessary. Another possibility is that modification of spider behavior is a relatively recently derived character in *H. argyraphaga*, but the probable plesiomorphic status of this species within *Hymenoepimecis* (Gauld 2000) and the ability of *H. tedfordi* to modify the behavior of *L. mariana* (W. Eberhard, in prep.) argue against this idea.

Neither Bignell (1898) nor Nielsen (1923) mention modified spider webs in most of the polysphinctine larvae they studied, but Shaw (1994:125) states that "many spiders about to succumb to polysphinctines seek a concealed site into which they spin themselves". Nielsen (1923) noted that the last web that the host *Cyclosa conica* (Pallas) made before pupation by *Polysphincta nielseni* Roman was unusually small, and that such small orbs were especially resistant to damage. In contrast, he noted an apparently normal web of a "certain *Theridia*" with the cocoon of a *Acrodactyla degener* (Haliday) (Nielsen 1923). The web of the theridiid "*Theridion*" with the cocoon of a *Zatypota albicoxa* that he figured (Nielsen 1923) also seems normal, while Jimenez (1987) states that *Zatypota* sp., which parasitizes *Theridion contreras*, attaches its cocoon to the substrate rather than suspending it in the web. I have seen the cocoon of an unidentified species of *Zatypota* in an apparently unmodified web of its theridiid host, *Anelesimus* sp. These sparse data thus suggest

the preliminary conclusion that the non-orb webs in which these wasps pupate are not modified. A possible variation is *Polysphincta tuberosa* Gravenhorst, which parasitizes the orb weaver *Araneus quadragatus*; but, judging from the figure of the cocoon and an accompanying web (Nielsen 1923), this species may pupate in the silk retreat made by the host (Jones 1983) rather than on the orb. Much more work remains to clarify the evolution of the ability of these larvae to manipulate host web spinning behavior.

The failure of female *H. argyraphaga* to use the ovipositor for oviposition resembles oviposition in aculeate wasps. Similar, presumably convergent oviposition direct from the genital opening has been seen in an unspecified adelognathine ichneumonid, and is suspected in the braconid *Histeromerus* (Shaw 1995). The ovipositor of *H. argyraphaga* also injected paralyzing venom into the spider host, and the attacking wasp probably stabs the spider with her unsheathed ovipositor during the instant she is landing and seizing it. In addition, the ovipositor was used to pry eggs and larvae of previous females from the spider's abdomen, and may also be used to sting these larvae. Live larvae are difficult to pry from the spider. One of the distinguishing traits of Polysphinctini in general is a very sharply pointed ovipositor (Fitton et al. 1988). It is tempting to suppose that the sharp point is an adaptation to aid rapid penetration and immobilization of spider hosts, which are potentially dangerous hosts.

Most European polysphinctines appear to oviposit at rather consistent sites on their hosts (Shaw 1998), but extensive descriptions of intra-specific variation in oviposition sites on their host (e.g., Fig. 3) are not available for other polysphinctines, so it is not clear whether the substantial variation in *H. argyraphaga* is unusual. It is possible that selection to escape infanticide by subsequent females favors variation in where eggs are placed on the spi-

der. The larger larvae won out over smaller individuals in two cases in which two larvae grew on the same host.

Selection on spiders.—The success of attacks by *H. argyraphaga* depended on the wasp grasping the spider through the web as it rested at the hub of its orb. Both the spider's observed defensive behavior (dropping quickly on a drag line below the orb in response to the wasp's approach from above), and the circumstances in which some wasp attacks failed (when the wasp hit the orb too far from the spider to grasp it) support the old idea that meshes of lines associated with orb webs function to defend the spider from enemies (summaries in Lubin et al. 1982, Eberhard 1990). The strategy of attacking the spider from above functions well with the more or less horizontal orbs of *P. argyra*, but leaves the wasp unable to follow the spider down its drag line when it drops, as Bignell (1898) observed an unidentified polysphinctine to do by walking down the line.

This limitation on wasp attacks makes it difficult to explain why late instar and mature female *P. argyra* seldom spin a mesh above or below the orb. Such meshes often occur in the web of earlier instars of this species. Among 31 webs of as many adult females, 90% lacked any mesh above the orb, while the corresponding frequency for 52 penultimate nymphs was 65% ($p = 0.05$ with χ^2). Unpublished data from student projects strongly suggest that spiders build such meshes even more frequently in earlier instars. The phylogeny proposed for *Plesiometa*, *Leucauge*, and related genera (Hormiga et al. 1995) suggests that mesh construction is a derived trait in these two genera.

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